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RESEARCH ARTICLE

Natural deadwood hosts more diverse pioneering wood-inhabiting fungal communities than restored deadwood

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Deadwood can be recreated as a forest restoration measure to increase the amount of deadwood and assist deadwood-dependent biodiversity. While deadwood restoration is known to have an overall positive effect on associated species in the long term, it remains poorly understood how and when wood-inhabiting organisms colonize different kinds of deadwood, which is essential for developing efficient restoration frameworks. In this study, we use DNA metabarcoding to compare wood-inhabiting fungal communities between fresh naturally fallen spruce logs and spruce logs felled for restoration. The results show that although pioneering fungal community composition greatly differs between natural and felled logs, with natural logs hosting more species-rich and heterogeneous communities, felled logs still hold a relatively high fungal diversity. Responses to log type carried a strong phylogenetic signal, and orders Polyporales and Hymenochaetales including most species of conservation concern were more likely to occur in natural than in felled logs. Furthermore, we found that log type was more important for rarely recorded than commonly recorded taxa, suggesting that rare species might be more specialized in their habitat requirements than the common ones. Overall, while restored deadwood can hold a high fungal diversity, the results underline that freshly felled logs do not mimic fresh natural logs. Deadwood restoration should focus not only on increasing the quantity of deadwood but also on the quality of thereof, and most importantly, retaining the existing natural deadwood rather than artificially downing trees.

Key words: colonization, deadwood restoration, ecological restoration, metabarcoding, mortality factor, saproxylic

Implications for Practice

- When creating deadwood as a restoration practice, it is critical to monitor species' colonization patterns from the beginning, as wood-inhabiting communities are known to follow strong priority effects. Thus, if pioneering communities in created deadwood are different from the ones in natural deadwood, these differences may persist through time with potential implications for the forest diversity.
- Differences in the pioneering fungal communities between fresh natural and felled logs demonstrate that from the very beginning, artificial substrates do not fully mimic natural substrates. Therefore, in addition to increasing the deadwood quantity, effective deadwood restoration should focus in recreating the quality of natural deadwood. Additionally, preserving existing natural deadwood should be prioritized in order to support wood-inhabiting fungal diversity as a whole.

Introduction

Human land use activities have led to a global degradation of forest ecosystems (Foley et al. 2005). In boreal forests, forest management for timber is one of the main drivers of forest degradation (Gauthier et al. 2015; Curtis et al. 2018). Management activities have greatly reduced the cover of older forest areas across the boreal biome (Gauthier et al. 2015) and drastically homogenized the overall forest structure, especially in countries with intensive management for industrial wood production (Östlund et al. 1997; Gauthier et al. 2015; Martin et al. 2020). As a result, remaining forest areas lack natural complexity and are poorer in the diversity of habitats they provide to forest-dwelling organisms (e.g. Kuuluvainen 2002, 2009). Deadwood

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is an essential habitat for thousands of forest species, ranging from fungi to arthropods (Siitonen 2001; Stokland et al. 2012). Alarmingly, deadwood has decreased both in quantity and quality due to forest management (Fridman & Walheim 2000; Siitonen 2001; Similä & Junninen 2012) which compromises the capability of forest areas to maintain their local species diversity (Paillet et al. 2010; Lassauce et al. 2011; Hyvärinen et al. 2019). In Finland, for example the decreased amount of deadwood is one of the major threats for forest species (Hyvärinen et al. 2019), many of which have functionally crucial roles in forest ecosystems through decomposition and nutrient cycling (Stokland et al. 2012).

Ecological restoration is a tool applied to counteract forest degradation and to artificially introduce natural resources back to ecosystems (Halme et al. 2013; Stanturf et al. 2014). Currently in Europe, ecological restoration is extremely topical due to the European Commission's proposal for a Nature Restoration Law as a part of the EU Biodiversity Strategy (European Commission 2022). In the proposal, increasing the availability of deadwood is included as a central element for the restoration of forest ecosystems. Deadwood can be restored by felling, uprooting and girdling trees among others (Virnes et al. 2012). The importance of applying a mix of restoration methods has been emphasized, as from the species perspective, different methods create deadwood resembling natural deadwood with differing qualities (Virnes et al. 2012; Pasanen et al. 2018). Deadwood restoration has been an established management tool especially in managed forests but the lack of deadwood is not exclusive to them; many currently protected areas also have a deficit of deadwood due to past management actions (Similä & Junninen 2012).

Wood-inhabiting fungi require deadwood as their habitats and have therefore been particularly affected by forest management (Lonsdale et al. 2008; Junninen & Komonen 2011; Tomao et al. 2020). A large body of literature has reported declines in wood-inhabiting fungal diversity in managed forests compared to unmanaged forests (e.g. Penttilä et al. 2004; Abrego & Salcedo 2013; Juutilainen et al. 2014). Fungi that require large logs are especially negatively affected by forestry actions (Penttilä et al. 2006; Nordén et al. 2013; Abrego et al. 2017), as due to management practices large-sized deadwood has disproportionately declined compared to fine-sized deadwood (Siitonen et al. 2000; Gibb et al. 2005).

Many previous experiments have revealed an overall positive effect of deadwood restoration on the abundance and richness of wood-inhabiting fungi (reviewed in Sandström et al. 2019). However, not all wood-inhabiting fungal species are affected in the same way. While many studies have found a greater average abundance and richness of wood-inhabiting fungi in restored than in natural deadwood (Komonen et al. 2014; Pasanen et al. 2014, 2018; but see Elo et al. 2019), the communities in the restored deadwood tend to be more homogeneous and dominated by common species (Komonen et al. 2014; Pasanen et al. 2014, 2018; Elo et al. 2019) and at least in the short term, rare and red-listed species are rarely recorded (Komonen et al. 2014; Pasanen et al. 2014; Sandström et al. 2019; but see Pasanen et al. 2018). Previous studies have hypothesized that this is mainly due to the lack of habitat heterogeneity in restored deadwood (Komonen et al. 2014; Elo et al. 2019). The way the tree dies (i.e. mortality factor) affects its quality as deadwood and, therefore, which fungal species are able to colonize the resource (Renvall 1995; Boddy & Heilmann-Clausen 2008; Stokland & Siitonen 2012), potentially leading to differing species composition in restored compared to natural deadwood.

The ability of different fungi to colonize deadwood with different mortality factors may explain why restored deadwood does not fully mimic natural deadwood. With time, community differences observed among early colonizers might become even more pronounced through priority effects where the pioneer communities influence the later-arriving species (Fukami et al. 2010). Many previous studies on deadwood restoration and wood-inhabiting fungi have been conducted years after the restoration activities took place and have been based on fruit-body surveys (e.g. Komonen et al. 2014; Pasanen et al. 2014; Elo et al. 2019). Therefore, it remains unclear if the previously reported community differences between natural and restored deadwood already exist among the pioneer fungi present as mycelia. In fallen logs, pioneering fungal communities are mainly composed of species occurring as latent propagules already in living trees and species which quickly colonize the logs after treefall (Boddy 2001; Parfitt et al. 2010; Gilmartin et al. 2022).

To shed light on the first stages of community succession and assess the effectiveness of deadwood restoration in supporting fungal diversity, we asked whether and how pioneering fungal communities differ between natural and restored deadwood. We applied DNA metabarcoding to characterize wood-inhabiting fungal communities in fresh naturally fallen and felled Norway spruce logs at five Finnish forest sites. We asked (1) are the pioneering fungal communities different between natural and felled logs in terms of species' composition and richness; (2) are such community differences phylogenetically structured; and (3) do rare taxa show more specialized log type preferences than common fungal taxa. We expected that fresh natural logs hold higher fungal species diversity and abundance than recently felled logs due to the more advanced community succession through natural mortality and the higher habitat complexity. Particularly, we expected the fungal groups including species of conservation concern to be less common in the felled logs. We however expected that felled logs still hold a high species diversity as many fungal species may colonize the trees while the latter are still alive or they might host fast-colonizing species (Boddy 2001).

Methods

Study Sites

We conducted the study at five forest sites in southern and central Finland in northern Europe that were located in the southern and middle boreal zones (Table 1; Fig. 1A; Ahti et al. 1968). The sites included one national park and four set-aside forests (Table 1). We selected sites that were dominated by Norway spruce (*Picea abies* [L.] Karst.). All sites were formerly managed, but no forest management activities have been carried out in them over the last decades. Consequently, all sites were abundant in deadwood and had a middle-aged or mature stand structure (Table 1). Depending on the availability of suitable study logs, the size of experimental area varied between 2 and

Table 1. Information on the study sites located in Finland. Experimental area size is the area (ha) covered by study logs within each study site accounting for a 20-m buffer surrounding each study log. Mean stand age was derived from Natural Resources Institute Finland (2019) by averaging stand age for an area that comprised a 50-m buffer around each study log.

	Site	*Municipality*	*Bioclimatic zone*	*Site type*	*Experimental area size (ha)*	*Mean stand age (year)*
1	Kesijärvi	Janakkala	Southern boreal	Set-aside forest	2	58
2	Lapinjärvi	Lapinjärvi	Southern boreal	Set-aside forest	4	64
3	Luukki	Espoo	Southern boreal	Set-aside forest	5	89
4	Seitseminen	Ylöjärvi	Middle boreal	National park	4	83
5	Sääjärvi	Janakkala	Southern boreal	Set-aside forest	5	72

5 ha (Table 1). See Supplement S1 for details on the study site managers and owners.

Study Design

Our study included naturally fallen spruce logs (henceforth called natural logs) and spruce logs felled for restoration (henceforth called felled logs) (Fig. 1B). In April–May 2019, we randomly selected 37 living spruces at each study site and cut them from the base with a chainsaw. We only chose spruces with ≥20 cm diameter at breast height (DBH), except for the site in Lapinjärvi where larger trees were scarce, we also chose one log with DBH 18 cm and five logs with DBH 19 cm (average DBH for all felled logs 28.2 ± 4.6 cm). In August–October 2019, we selected 55 natural logs at each site that had fallen either by breakage or uprooting (50 and 50% of all natural logs, respectively). To match the felled logs which all represented decay stage 1, we only selected recently dead or slightly decayed natural logs in decay stages 1 and 2 (scale from 1 to 5 where 1 corresponds to recently dead log with hard wood, and 2 corresponds to slightly decayed wood where knife penetrates 1–2 cm; Renvall 1995). Out of all natural logs, 65 and 35% belonged to decay stages 1 and 2, respectively. We applied the same ≥20 cm DBH threshold as for felled logs, except for two

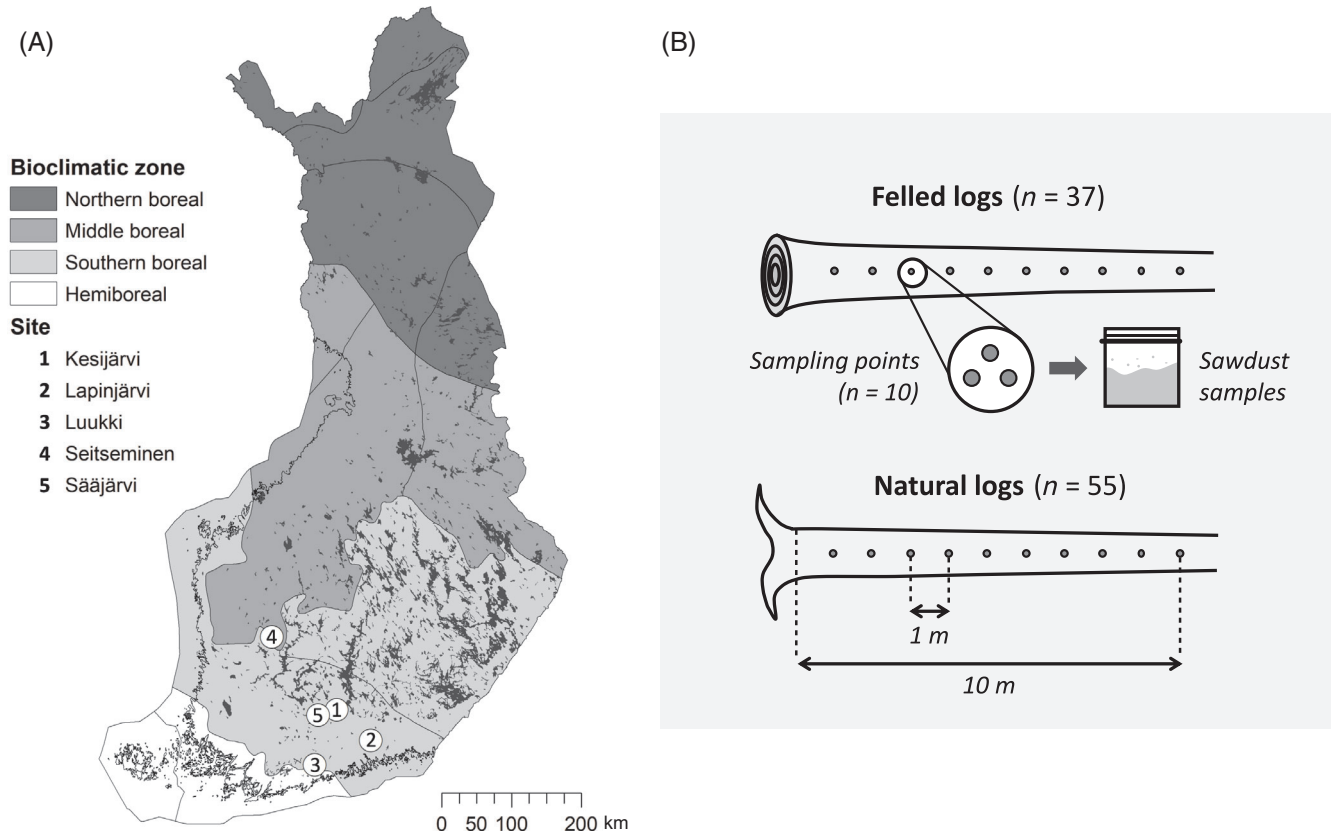

Figure 1. Location of the study sites in Finland (A) and the study design (B). In panel (A), the bioclimatic zones (Ahti et al. 1968) are indicated in greyscale. Panel (B) illustrates the study design carried out in each of the study sites. The design included both felled and natural study logs. From each log, we collected sawdust from 10 sampling points (indicated with dots) starting 1 m from the base and continuing at 1-m intervals. At each sampling point, sawdust samples were collected from three holes and pooled in one ziplock bag. © Finnish Environment Institute 2020 (bioclimatic zones), National Land Survey of Finland 2019 (waterways).

logs with DBH 18 and 19 cm in Lapinjärvi (average DBH for all natural logs 28.5 ± 6.2 cm). All logs were spatially distributed as evenly as possible within the study site, and they preferably did not touch each other. In cases where we had to select two intersecting logs, we only allowed them to intersect after 10 m from the base where no sawdust samples were collected. Altogether, we sampled 275 natural and 185 felled logs.

Collection of Sawdust Samples

We sampled the mycelial communities in August–October 2019. We collected sawdust samples by drilling the study logs and collecting the resulting sawdust in plastic ziplock bags. From each log, we collected sawdust from 10 sampling points starting 1 m from the base (or root collar in the case of uprooted logs) and continuing with 1-m intervals (Fig. 1B). At each sampling point, we collected sawdust from three holes drilled in a triangular shape (ca. 3 cm apart) in one bag (Fig. 1B), resulting in 10 samples per log. We used a 11 × 105 mm drill bit and a Makita cordless drill (model DDF481). All samples were collected from the same side of the log by drilling perpendicularly toward the log center. Before drilling, we removed bark from the sampled area to avoid collecting fungal DNA not occurring as mycelia. To avoid cross-contamination, we wiped the remaining sawdust off the drill bits, soaked them in a 5% sodium hypochlorite, rinsed with water and soaked them in ethanol after each log.

Measured Log Characteristics

As the main variable of interest, we recorded log type indicating whether the log was natural or felled. We further grouped natural logs into broken and uprooted logs according to their mortality factors. While the time since felling was approximately 4 months for felled logs, no such information existed for natural logs. Therefore, we used decay stage (1 or 2) as the criterion for ensuring that natural logs represented logs with pioneering wood-inhabiting fungal communities. Additionally, we measured DBH (cm), the proportion of log surface with ground contact and bark cover (0–100% in steps of 10%), and canopy openness (0–100%) above each log. Canopy openness was measured by taking a photo of the canopy with a fisheye lens while standing on top of the log 5 m from the base, and calculating the proportion of sky pixels in each photo using ImageJ (following Oldén et al. 2017). Site-level summary of log characteristics is presented in Table 2.

Sample Pre-Processing, DNA Extraction, Sequencing, and Bioinformatic Analyses

Here, we summarize the protocols for sample pre-processing, DNA extraction, sequencing, and bioinformatic analyses which are described in full detail in Supplement S2. Sawdust samples were first pre-processed at the University of Helsinki, Finland. We pooled the sampling-point specific samples to obtain one sample per log, freeze-dried the samples, and pulverized them with a homogenizer and metal beads.

Sample lysis, DNA extraction, and polymerase chain reaction (PCR) amplifications were completed at the Canadian Centre for DNA Barcoding, while next generation sequencing of indexed amplicon libraries was run at the Advanced Analysis Centre at the University of Guelph, Canada. We added insect lysis buffer with 1% polyvinylpyrrolidone and proteinase K to each sample. A subsample of the lysate was mixed with plant binding buffer and transferred onto a glass fiber (GF) plate (PALL) to bind DNA with the membrane. Two DNA washes were conducted by centrifuging with the plant binding buffer followed by plan protein wash buffer. Final wash was repeated twice, and then the GF plate was incubated. DNA was eluted from dried membrane with TrisHCL and centrifugation. We completed the PCRs in 96-well format using standard CCDB Platinum Taq Master Mix with primers ITS3-misN6 and ITS4-misN6 from Ovaskainen et al. (2020). We ran two rounds of PCR, second of which was indexing round with fusion primers with standard i5 and i7 Illumina indices. We visualized the amplicons using bufferless *E*-gel system (Invitrogen) after PCR. Before sequencing, we pooled the amplicons from each well, purified, and quantified them on a Qubit 2.0 fluorometer and checked for size on Agilent Bioanalyzer. Sequencing was performed on Illumina MiSeq with PE2x300 following standard manufacturer's protocol.

We performed bioinformatic analysis using a development version of the OptimOTU pipeline, implemented in R version 4.0.5 (R Core Team 2021). First, we completed initial trimming and filtering with Cutadapt version 4.0 (Martin 2011) by demultiplexing paired end fastq files, trimming both *R*1 and *R*2 reads to remove multiplexing indices at both ends, and removing both reads if either read containing "*N*" bases or had length less than 100 bp. Next, we performed an additional round of filtering in DADA2 version 1.18 (Callahan et al. 2016) to remove read pairs with high expected error-rate, and to remove any reads mapping to the PhiX genome. Then we dereplicated, denoised, merged, and chimera filtered the reads for each run independently according to the standard DADA2 ITS pipeline (Callahan 2020). We taxonomically identified the remaining amplicon sequence variants (ASVs) using Protax-Fungi, which assigns taxonomic identities at ranks from phylum to species along with well-calibrated probability estimates that each identity at each rank is correct (Abarenkov et al. 2018). We considered the classifications reliable if the probability exceeded 90%. At each rank, we clustered the ASVs using taxonomically informed pseudo-single-linkage clustering. We formed the reference cluster cores, matched and joined the unidentified sequences to cluster cores using the -usearch_global command in VSEARCH version 2.15.2 (Rognes et al. 2016), and single-linkage clustered the remaining unclustered ASVs using BLASTCLUST version 2.2.26 (Dondoshansky & Wolf 2000) and USEARCH version 11.0.667 (Edgar 2010). We determined optimal clustering thresholds at each rank using the hierarchical optimization technique developed by Dnabarcoder (Vu et al. 2022) except using the same USEARCH + BLASTCLUST single-linkage clustering. We used taxonomically identified fungal sequences from the Global Spore Sampling Project (Ovaskainen et al. 2020) as references for the threshold optimization step. Finally, we chose the remaining clusters at the species rank as our primary unit of ecological analysis, and refer to these as operational taxonomic units (OTUs).

Table 2. Mean values and standard deviations for the log characteristics at each study site. Sample sizes were 55 for natural logs (including both broken and uprooted logs) and 37 for felled logs per site. Mortality factor indicates whether the natural logs have fallen by breaking or uprooting. DBH is the log diameter measured at breast height (1.3 m). Ground contact is the proportion of the log touching the ground, bark cover is the proportion of log surface covered by bark, and canopy openness is the proportion of visible sky above the log.

Site	*Log type*	*Mortality factor*	n	*DBH (cm)*	*Decay stage*	*Ground contact (%)*	*Bark cover (%)*	*Canopy openness (%)*
Kesijärvi	Natural	Broken	1	24.0	1.0	0.0	100.0	49.4
	Natural	Uprooted	54	26.5 ± 3.9	1.4 ± 0.5	13.3 ± 16.4	87.7 ± 19.3	42.6 ± 16.5
	Felled	—	37	29.6 ± 4.4	1.0 ± 0.0	27.3 ± 26.4	90.4 ± 16.4	27.7 ± 12.5
Lapinjärvi	Natural	Broken	34	24.6 ± 3.8	1.1 ± 0.4	12.4 ± 14.4	44.1 ± 32.9	35.4 ± 12.2
	Natural	Uprooted	21	32.4 ± 8.6	1.1 ± 0.4	10.0 ± 12.2	72.9 ± 22.2	31.3 ± 9.4
	Felled	—	37	24.0 ± 4.6	1.0 ± 0.0	9.5 ± 10.0	68.6 ± 27.7	30.6 ± 11.8
Luukki	Natural	Broken	30	28.7 ± 5.8	1.4 ± 0.5	19.0 ± 25.4	33.0 ± 25.5	24.3 ± 6.8
	Natural	Uprooted	25	35.7 ± 6.4	1.6 ± 0.5	10.0 ± 21.2	31.2 ± 27.0	24.8 ± 7.4
	Felled	—	37	29.9 ± 4.6	1.0 ± 0.0	16.8 ± 19.2	46.8 ± 24.8	22.6 ± 5.2
Seitseminen	Natural	Broken	49	30.4 ± 5.3	1.3 ± 0.5	19.4 ± 19.9	63.3 ± 28.1	31.7 ± 9.9
	Natural	Uprooted	6	32.0 ± 3.2	1.3 ± 0.5	21.7 ± 35.4	86.7 ± 13.7	33.6 ± 5.4
	Felled		37	28.7 ± 3.6	1.0 ± 0.0	31.1 ± 23.7	95.4 ± 9.6	26.5 ± 5.7
Sääjärvi	Natural	Broken	23	24.2 ± 3.1	1.2 ± 0.4	15.7 ± 19.7	31.7 ± 31.1	31.0 ± 14.5
	Natural	Uprooted	32	27.6 ± 5.9	1.5 ± 0.5	15.3 ± 18.8	54.1 ± 32.2	30.5 ± 10.0
	Felled	—	37	28.6 ± 3.5	1.0 ± 0.0	24.3 ± 21.3	83.2 ± 22.7	28.7 ± 9.2

Statistical Analyses

We constructed an OTU x sampling unit data matrix where the matrix elements describe the number of fungal sequence reads assigned to each OTU in each sample, and sampling units correspond to individual logs. The original community data consisted of 2174 OTUs occurring in 460 sampling units. For the analyses, we excluded two sampling units with sequencing depth less than 5000 and one sampling unit with no fungal reads, resulting in 2170 OTUs and 457 sampling units.

To visualize the general patterns of community composition, we illustrated community differences with the R package metacoder (Foster et al. 2017) and applied non-metric multidimensional scaling (NMDS) using the R package vegan (Oksanen et al. 2022). With metacoder, we estimated differences in the relative read abundance (RRA, number of reads per OTU divided by the total number of reads per sample; Deagle et al. 2019) between samples from different log types for each taxon using the function compare_groups() with Wilcoxon rank sum test and correction for multiple comparisons with false discovery rate. We plotted taxonomic trees and visualized taxonomic differences between log types based on log2 ratio of median abundances using the function heat_tree_matrix(). For NMDS, we applied a three-dimensional ordination on a sample-level with Bray–Curtis dissimilarity based on RRA with the function metaMDS(), and visualized the ordination solution with the lowest stress value with the R package ggplot2 (Wickham 2016).

To examine how wood-inhabiting fungal communities responded to log type and other log characteristics, we analyzed the community data with the joint species distribution modeling framework named hierarchical modeling of species communities (HMSC; Ovaskainen et al. 2017; Ovaskainen & Abrego 2020). To avoid multicollinearity, we assessed the relationships between the measured log characteristics before the statistical modeling (described in Supplement S3).

Due to the zero-inflated nature of the data, we fitted a hurdle-type model consisting of two parts: presence–absence (modeled with probit regression), and abundance conditional on presence (modeled with log-normal regression, with absences declared as missing data). We note, however, that read counts do not directly translate into species' abundances due to the biases related to sequence data sets (Amend et al. 2010; Deagle et al. 2019). For both model parts, as fixed predictors we included log type (categorical variable with two levels), mortality factor (categorical variable with two levels), DBH (continuous variable), decay stage (continuous variable), ground contact (continuous variable), and log-transformed sequencing depth (i.e. number of reads per sample, continuous variable). For log type, we defined a categorical variable with levels natural and felled, where the level natural included both broken and uprooted logs which categories were missing for felled logs. To examine the importance of mortality factor, we defined mortality factor to have value of −0.5 for broken logs, the value of 0.5 for uprooted logs, and the value of 0 for felled logs. To account for the study design, we also included the random effect of site. Based on exploratory analyses, we excluded bark cover and canopy openness from the models because of their associations with log type (Supplement S3). To examine whether the variation among the species in their environmental responses co-varied systematically with their phylogeny, we included a taxonomic tree in the model where we assumed equal branch lengths for each taxonomic level.

We constructed the main model for those 263 OTUs that occurred in at least 20 sampling units (henceforth called common OTUs), thus leaving out 1907 OTUs with fewer occurrences (henceforth called rare OTUs). To ask whether the rare OTUs showed different responses than the common OTUs, we jointly modeled the species richness of common and rare OTUs on a log-level with a bivariate Poisson regression model. This species richness model included the same fixed and random

effects as the main model (fixed effects log type, mortality factor, DBH, decay stage, ground contact, and sequencing depth, and site as a random effect). To test for the robustness of our results regarding the occurrence threshold, we ran the same set of analyses with two alternative thresholds and included those OTUs that occurred at least 10 (450 OTUs) or 50 times (108 OTUs) in the data. Results for these alternative models are provided in Supplement S4. Additionally, to check that the effects of log type were not confounded with the variation in decay stage in natural logs, we fitted alternative models which excluded natural logs in decay stage 2 (and therefore did not include decay stage as a predictor). Results for the latter alternative models are provided in Supplement S5.

We fitted both the main model (consisting of presence–absence and abundance conditional on presence parts) as well as the species richness model with the R package Hmsc (Tikhonov et al. 2020) assuming the default prior distributions (Ovaskainen & Abrego 2020, pp. 184–216). We sampled the posterior distribution with four Markov Chain Monte Carlo (MCMC) chains, each of which was run for 37,500 iterations, of which the first 12,500 were removed as burn-in. The chains were thinned by 100 to yield 250 posterior samples per chain and thus 1000 posterior samples in total. We examined MCMC convergence by the potential scale reduction factors (Gelman & Rubin 1992) of the model parameters. Results for the MCMC convergence are provided in Supplement S6.

The explanatory power of the HMSC models was assessed through AUC (Pearce & Ferrier 2000) and Tjur's R^2 (Tjur 2009) for presence–absence part of the main model, through R^2 for abundance part of the main model, and through pseudo-R^2 for the species richness model. We applied variance partitioning to calculate the proportion of explained variance in species occurrences, abundances, and species richness attributed by each model predictor (Tikhonov et al. 2020). We also evaluated posterior support for the beta parameters that describe OTU-level responses to each model predictor in the main model, and responses of common and rare OTUs in the species richness model. To examine if phylogenetically related OTUs showed similar responses to the predictors, we examined the level of taxonomic signal in the beta responses of the main model through the parameter rho (Ovaskainen & Abrego 2020). We then examined which orders showed systematic responses to log type. We conducted all statistical analyses using R version 4.2.0 (R Core Team 2022).

Results

Overall Fungal Community Composition

Out of all recorded fungal OTUs ($n = 2170$), 59.8% (RRA = 0.60) were assigned to phylum Ascomycota, 38.2% (RRA = 0.38) to phylum Basidiomycota, 1.4% (RRA = 0.02) to phylum Mucoromycota, 0.4% (RRA = 9×10^{-5}) to Chytridiomycota, and the remaining 0.2% (RRA = 7×10^{-6}) were not taxonomically assigned with a 90% probability threshold. Considering lower taxonomic levels, 72.0% of the OTUs were successfully assigned to class, 61.5% to order, 45.0% to family, 32.9% to genus, and 9.7% to species.

Regarding the log type distribution of OTUs, 55% of the OTUs were unique to natural logs and 16% to felled logs, while 29% of OTUs occurred in both log types. Among the OTUs unique to natural logs, 39% were only recorded in broken logs, 32% only in uprooted logs, and the remaining 29% occurred across both mortality factors. Based on RRA, orders Helotiales, Hymenochaetales, Hypocreales, and Polyporales were more abundant in both types of natural logs relative to felled logs, while orders Agaricales, Microascales, Ophiostomatales, Pleosporales, and Saccharomycetales were more abundant in felled logs (Fig. 2). On average, broken logs hosted 55.8 OTUs (SD ± 30.8), uprooted logs 53.2 OTUs (SD ± 37.2), and felled logs 43.6 OTUs (SD ± 24.5).

The NMDS ordinations showed a clear clustering of species composition according to different log types (Fig. 3). Communities in natural logs with different mortality factors showed partial overlap while communities in felled logs were clearly grouped separately. Natural logs in decay stage 1 were located slightly closer to the felled logs than natural logs in decay stage 2 for both broken and uprooted logs (Fig. 3). Natural logs in decay stages 1 and 2, however, did not clearly separate in the ordination space.

Explaining Variation in Fungal Community Composition

The average explanatory power for presence–absence part of the main model was 0.80 measured with the AUC and 0.14 measured with the Tjur R^2, and for abundance conditional on presence part, 0.20 measured with R^2. Log type was the most important model predictor for both fungal occurrences and abundances conditional on presence (Table S1). The proportion of explained variance attributed to log type was two times more for occurrences than for abundances. Compared to log type, mortality factor was less important for abundances and even more so for occurrences (Table S1). The random effect of site was the second most influential variable after log type affecting both occurrences and abundances (Table S1). The remaining predictors—DBH, decay stage, ground contact, and sequencing depth—captured only one-fifth of the explained variance in occurrences, though they explained twice as much variance in abundances (Table S1).

OTU-Level Responses to Predictors

Beta parameters of the main model describing how each OTU responded to each model predictor also highlighted the importance of log type: based on presence–absence part of the main model, more than 80% of OTUs had statistically supported responses (posterior probability ≥0.95) to log type (Fig. 4A). Two-thirds of these responses were positive indicating that more fungal OTUs occurred more likely in natural than in felled logs. Mortality factor had a weaker effect on occurrences: less than 40% of OTUs responded to mortality factor with a mix of positive and negative responses (Fig. 4A). The occurrence probability for OTUs with positive responses to mortality factor was

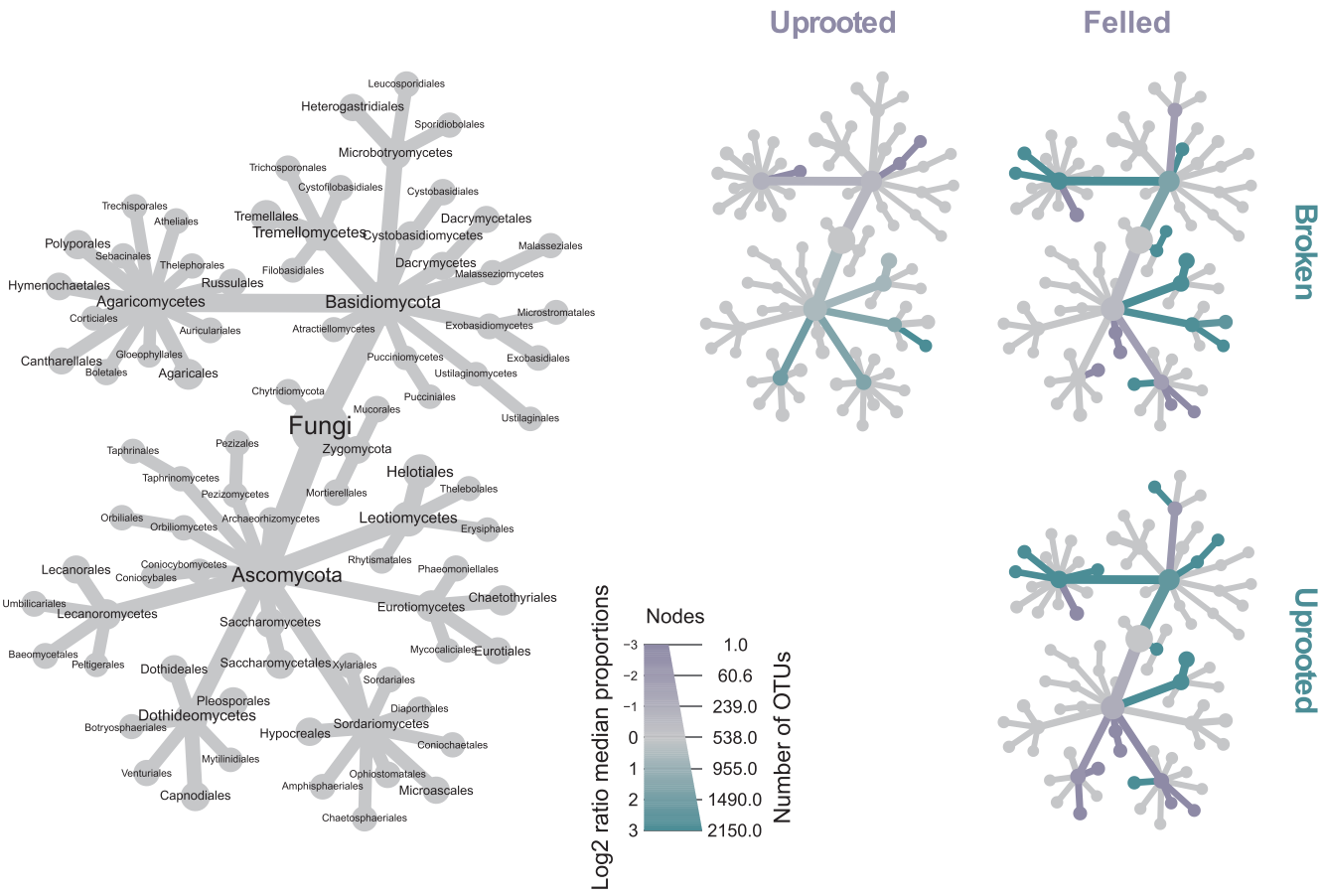

Figure 2. Taxonomic trees visualizing pairwise differences in the relative read abundance of wood-inhabiting fungal taxa in samples from the three different log types, that is felled and natural split into broken and uprooted according to their morality factor (resulting in three pairwise comparison). The two log types being compared with each taxonomic tree are indicated with the row and column labels. In each tree, differences between log types are shown with colors: a taxon colored purple is more abundant in samples from log type defined in the column, and a taxon colored green is more abundant in samples from log type defined in the row. Magnitude of difference is indicated with color shade so that larger differences are shown with darker colors. Taxonomic trees have been truncated to order level and taxon names are shown in the key on the left side of the plot. Node sizes are relative to the number of OTUs assigned to each taxon. Sample sizes for each log type and mortality factor were broken = 136, uprooted = 137, and felled = 184.

higher in uprooted than in broken logs, and the contrary for OTUs with negative responses.

Out of the remaining log characteristics, decay stage had the strongest effect on fungal occurrences with 37% of OTUs showing a statistically supported response (Fig. 4A). Responses were half positive and half negative, indicating that the responsive OTUs represent groups occurring more likely either in logs that have already started to decay or in freshly dead logs, respectively. OTU occurrences were mostly independent of DBH and ground contact, with only 16 and 8% of OTUs showing statistically supported responses to these characteristics (Fig. 4A). As expected, sequencing depth greatly influenced OTU occurrences positively (53% of the OTUs showed a statistically supported response; Fig. 4A) reflecting that the more sequences we obtain, the more likely we are to detect the species.

Abundance conditional on presence part of the main model yielded fewer statistically supported responses but the response patterns were generally consistent with the presence–absence part (Fig. 4B). OTUs had the largest number of statistically supported responses to sequencing depth (44% of OTUs) with only positive responses, and to log type (27% of OTUs) (Fig. 4B). As with the occurrences, there were almost twice as many OTUs that were more abundant in natural than in felled logs.

Phylogenetic Signal in OTU Responses

Parameter rho describing the strength of phylogenetic signal in OTU responses was statistically supported (posterior probability ≥0.95) for both presence–absence (posterior mean $\rho = 0.71$) and abundance conditional on presence (posterior mean $\rho = 0.97$) part of the main model. Namely, closely related OTUs had more similar responses to the model predictors than expected by random. We could separate three distinct groups based on occurrence responses to log type: Ascomycetes with positive and negative responses, and Basidiomycetes with positive responses (Fig. 4A). Out of the OTUs assigned to phylum

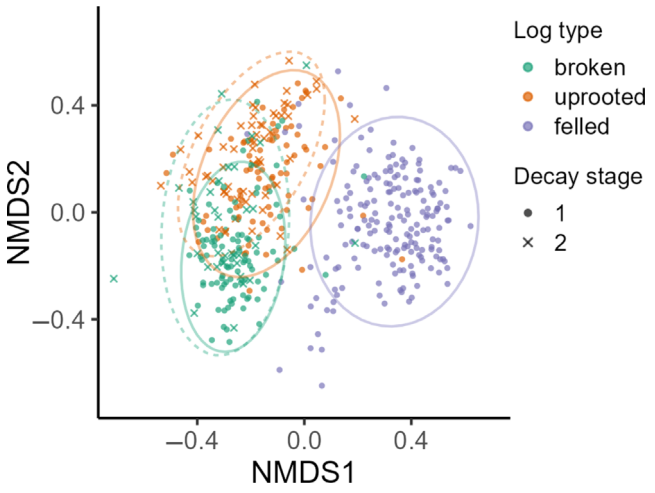

Figure 3. Two-dimensional representation of the three-dimensional NMDS ordination among wood-inhabiting fungal communities in individual logs (stress = 0.188, $n = 457$). Each point represents one log and its position in the ordination space. Points are colored by log type: natural log type that is further categorized by mortality factors broken and uprooted, and the felled log type. Logs in decay stage 1 are marked with circles and logs in decay stage 2 are marked with crosses. Ellipses encompass 95% of logs belonging to each log type × decay stage combination. Logs in decay stage 1 are marked with solid ellipses and logs in decay stage 2 with dotted ellipses. Plots for the additional axis combinations are provided in Figure S1.

Ascomycota, 47% were more likely to occur in natural logs and 34% in felled logs. Examples of ascomycetous orders that were more common in natural logs included Eurotiales, Helotiales, and Hypocreales, while orders such as Dothideales, Lecanorales, Pleosporales, and Saccharomycetales were more common in felled logs. Over 70% of OTUs assigned to phylum Basidiomycota were more common in natural than in felled logs, including orders such as Dacrymycetales, Hymenochaetales, Polyporales, and Tremellales. We could separate fewer taxonomic groups with uniform responses from abundance part of the main model (Fig. 4B), yet these groups were consistent with the groups detected in presence–absence part (Fig. 4A).

Comparing the Responses of Common and Rare OTUs

The average explanatory power for the species richness model was 0.14 measured with pseudo-R^2. The beta parameters showed that common and rare OTUs had largely consistent responses to the model predictors (Fig. 5). Species richness of both groups showed a statistically supported positive response to log type (posterior probability ≥0.95), indicating that both common and rare OTUs had higher species richness in natural than in felled logs (Fig. 5). The only difference between the groups was that the species richness of common OTUs was independent of mortality factor and DBH, while species richness of rare OTUs was higher in broken than in uprooted logs and increased with increasing diameter (Fig. 5). Both groups expressed positive responses to decay stage and sequencing depth and negative responses to ground contact (Fig. 5). By comparing the proportions of total variance attributed to each model predictor, we found that log type was more important for the species richness of rare than of common OTUs (Table S2). Sequencing depth was the most important model predictor for rare OTUs, while the random effect of site had the strongest effect on common OTUs (Table S2).

The results from the alternative model restricted to data with logs in decay stage 1 only (Supplement S5) were consistent with the results of the full models, supporting all the above reported results.

Discussion

By describing wood-inhabiting fungal communities at the earliest stages of community succession, we showed that although recently felled spruce logs hosted a relatively high variety of pioneering fungi, they did not support the full range of species hosted by fresh natural logs. Our results complement previous studies focusing on fungal communities in later stages (e.g. Komonen et al. 2014; Pasanen et al. 2014, 2018; Elo et al. 2019) and demonstrate that many of the reported community differences between natural and restored deadwood exist already among the pioneering fungal communities. Responses to log type were phylogenetically structured, with more taxonomic groups occurring more likely in natural than in felled logs. Finally, we showed that the species richness of both commonly and rarely recorded fungal OTUs was positively associated with natural log type but even more so for the rare taxa. Next, we explore each finding and discuss their implications for deadwood restoration.

Log Type Greatly Influenced Pioneering Fungal Communities

Our results showed that natural logs had a higher species richness of wood-inhabiting fungi and hosted over three times more unique fungal OTUs than felled logs. Consequently, the pioneering fungal community composition differed greatly between natural and felled logs, with natural logs holding more heterogeneous fungal communities than felled logs. Previous studies have also discovered natural deadwood hosting more variable communities than restored deadwood (Komonen et al. 2014; Pasanen et al. 2014, 2018; Elo et al. 2019), proposing that natural logs provide a wider range of microhabitats for fungi. However, some previous studies have reported restored deadwood hosting a higher species richness than natural deadwood (Komonen et al. 2014; Pasanen et al. 2014, 2018). For example, Komonen et al. (2014) found that the mean species richness of polypores was higher in felled than in natural logs of corresponding decay stage. Why our results showed the opposite is likely because we focused on freshly cut logs that have been available for fungal species for a short time window. Although the natural logs included in our study were also fresh, many of these have been available for fungal species for a longer time than felled logs and thus, succession of fungal communities in natural logs is likely more advanced than in felled logs (Boddy 2001).

We found two types of pioneering fungal species: those that were more likely to occur in natural logs and those that were more common in felled logs, potentially representing species

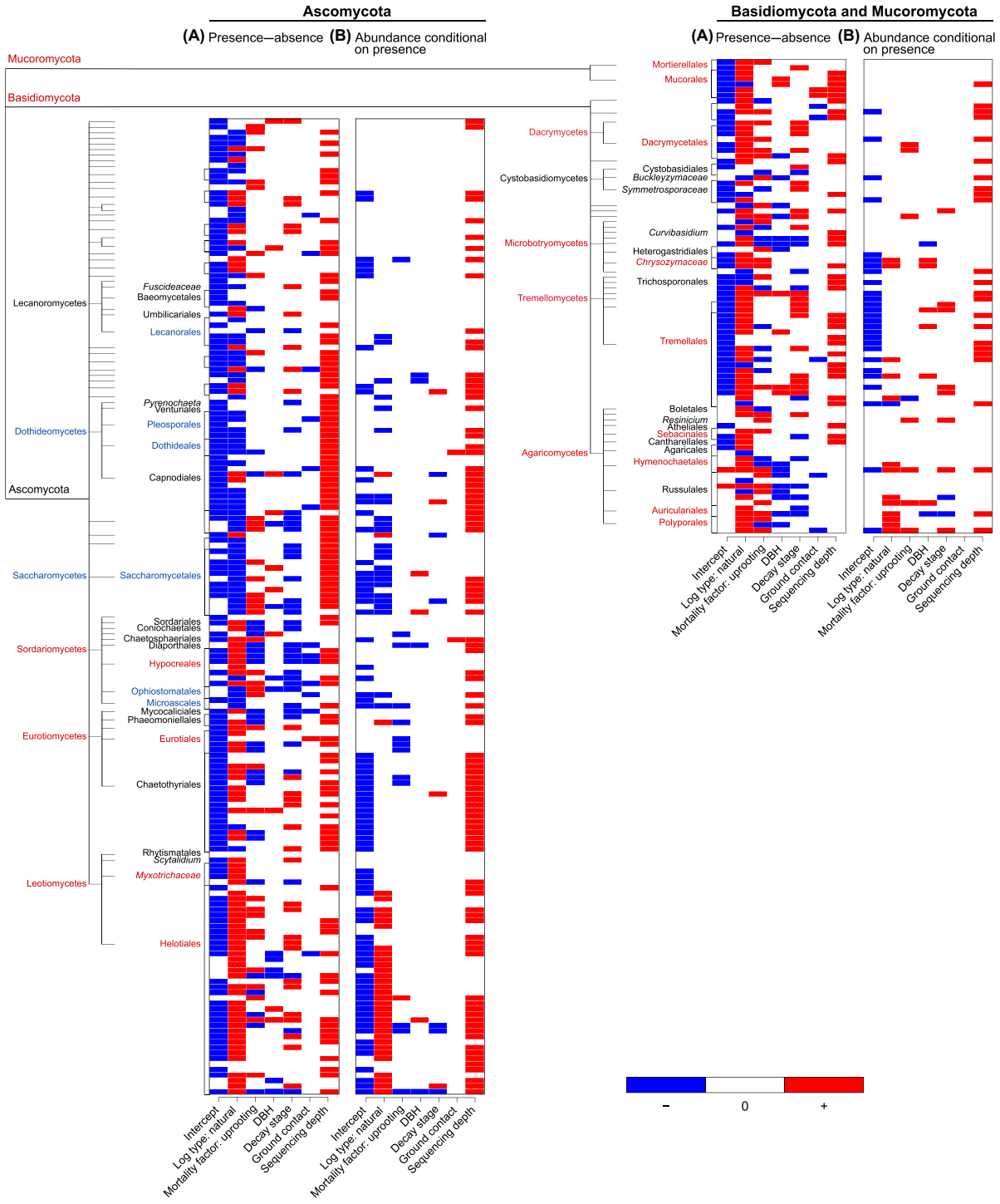

Figure 4. Estimated beta parameters describing OTU-level responses to environmental predictors in (A) presence–absence and (B) abundance conditional on presence parts of the main model. Felled log type and broken mortality factor are included as a reference level in the intercept. Positive and negative responses to model predictors with at least 0.95 posterior probability are indicated with red and blue colors, respectively. The remaining responses without strong statistical support are shown with white. Each line represents the responses of a single OTU. Order of the OTUs follows the phylogenetic relationship described with taxonomic trees. The first two panels on the left are for OTUs classified to phylum Ascomycota ($n = 177$) and the third and fourth panels for OTUs in phyla Mucoromycota ($n = 7$) and Basidiomycota ($n = 79$). Taxonomic trees are truncated to order level and names are displayed for described orders, classes, and phyla. We also included families which were listed as incertae sedis at the order level (italicized in the figure). Orders and classes without names are based on clustered yet unknown sequences. If occurrence of more than half of the OTUs belonging to a taxon show positive (negative) responses to log type, the taxon name is colored with red (blue) for taxa including ≥2 OTUs. OTUs belonging to same order are marked with square brackets. Taxonomic tree on species-level with all names is provided in Figure S2.

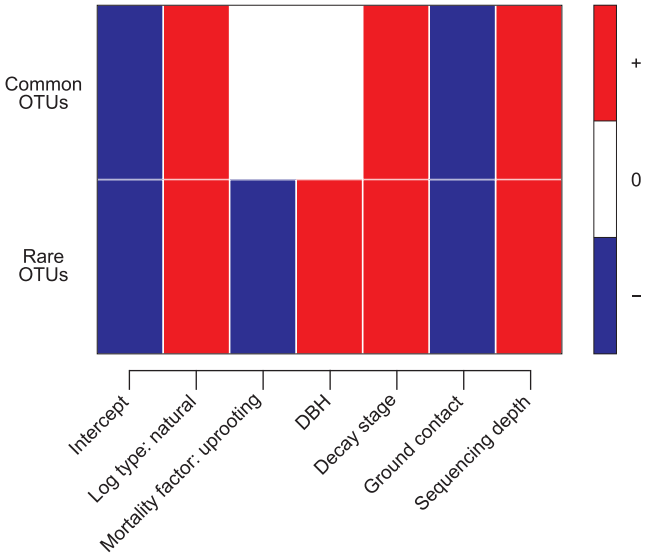

Figure 5. Estimated beta parameters for the species richness model. Beta parameters describe the responses to the environmental predictors separately for the species richness of common and rare wood-inhabiting fungal OTUs. Positive and negative responses to model predictors with at least 0.95 posterior probability are indicated with red and blue colors, respectively. The remaining responses without strong statistical support are shown with white. First row shows the responses of species richness of the common OTUs and second row the responses of species richness the rare OTUs.

with different habitat requirements. Fungal species that were more common in natural logs might require certain microhabitats only present in natural deadwood, such as slightly more advanced stage of decomposition (Hottola et al. 2009). Beyond direct requirements on their environment, these fungi might also be associated with certain species that must precede them before they can colonize the log (Niemelä et al. 1995; Abrego et al. 2017). On the other hand, fungi that were more dominant in felled logs might benefit from the relatively competition-free resource that these logs provided through a lower number of resident species. Pioneering fungal communities in felled logs have been associated with stress-tolerant and ruderal life strategies, both of which are usually combined with poor competitive abilities (Boddy 2001; Boddy & Hiscox 2016).

Furthermore, log type had a stronger effect on the species richness of rarely detected than of commonly recorded OTUs, suggesting that log properties are more important for rare than for common species. In the same line, previous studies have found that rare species are infrequently recorded in restored deadwood at least shortly after restoration (Komonen et al. 2014; Pasanen et al. 2014; Sandström et al. 2019). Together these results suggests that compared to common generalist species, rare wood-inhabiting fungal species might have more specialized habitat preferences (Hottola et al. 2009; Nordén et al. 2013) that might be harder to meet with restored deadwood.

Fresh Felled Logs Hosted a Relatively High Fungal Diversity

Felled logs hosted a surprisingly high diversity of fungal species despite the short time window they have been available for fungal colonization. According to Boddy (2001), pioneering communities in felled logs are mostly assembled by two groups of wood-inhabiting fungi. The first group is composed of latent fungi that occur as inactive propagules in the sapwood of living trees and start developing quickly after the tree is felled. The second group is represented by pioneer species that colonize the logs from the outside after it has fallen, either as spores from air or soil or as mycelia from soil. These species grow slower than the latent species that arrive first and thus, latent species can be assumed to be more represented in the communities of felled logs. Although some of these latent and fast-colonizing species are present also in natural logs, they hold a wider range of pioneer species as the decomposition is usually initiated by heart rot fungi and other pathogens already before they fall, supporting the diversity differences observed in our study.

Phylogenetic Signal in Fungal Responses

We found that the responses of fungal OTUs to log type were phylogenetically structured. Generally, OTUs assigned to phylum Basidiomycota were more likely to occur in natural than in felled logs, whereas OTUs in phylum Ascomycota covered taxonomic groups associated with both log types. Initial fungal communities in felled logs are known to be dominated by Ascomycetes but with initiated decay Basidiomycetes become increasingly more common (Chapela & Boddy 1988; Boddy 2001). Hence, ascomycetes that were more common in felled logs could represent latent species and other primary colonizers of freshly cut logs, while ascomycetes and basidiomycetes occurring more likely in natural logs could represent secondary colonizers and species specialized in microhabitats exclusive to natural logs. In fact, orders Polyporales and Hymenochaetales including several species of conservation concern (Kotiranta et al. 2019) were more common and abundant in natural logs, potentially indicative of more specialized habitat requirements of these species.

Broken and Uprooted Logs Hosted Rather Similar Fungal Communities

With natural deadwood, mortality factor is known to greatly affect the physiochemical properties of deadwood (Stokland et al. 2012) and consequently, which wood-inhabiting species will be able to colonize it (Renvall 1995; Boddy & Heilmann-Clausen 2008; Stokland & Siitonen 2012). In our study, however, mortality factor of natural logs did not have a strong effect on pioneering fungal communities. In line with this, in an European-level study, Abrego et al. (2015) found that broken logs held slightly but not significantly more fungal species than uprooted logs. However, many OTUs showed statistically supported responses to mortality factor, indicating that different mortality factors can create unique habitat properties critical for specific fungal groups.

On the Limitations of Our Study

Because, for practical reasons, it was not possible to track when the individual natural logs would fall, we used early decay stage as the variable representing pioneering wood-inhabiting fungal communities. Optimally, the natural logs would have fallen for exactly the same amount of time as the felled logs but in our case, most natural logs had probably fallen for a longer time. Natural logs have consequently experienced more time for fungal colonization than the felled logs, which may partially explain the found differences in the pioneering fungal communities between natural and restored deadwood. However, decay stage is known to be a highly influential variable for wood-inhabiting fungal communities (e.g. Rajala et al. 2015), and Norway spruce logs can stay at the initial decay stage (i.e. decay stage 1) for several years (Mäkinen et al. 2006). While we acknowledge that decay stage does not fully capture the time that the logs have been available for fungi, we consider that the variable still represents logs with pioneering fungal communities.

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Supporting Information

The following information may be found in the online version of this article:

Supplement S1. Information on study site managers and owners, and the felling treatment.
Supplement S2. Supplementary methods for sample pre-processing, DNA extraction, PCR, and bioinformatic analyses.
Supplement S3. Exploratory analyses of log characteristics.
Supplement S4. Robustness analyses with different occurrence thresholds.
Supplement S5. Robustness analysis with data restricted to logs in decay stage one.
Supplement S6. MCMC convergence.
Figure S1. NMDS ordination plots for additional axis combinations.
Figure S2. OTU-level taxonomic tree and species names for Figure 4.
Table S1. Results for the variance partitioning in the main model.
Table S2. Results for the variance partitioning in the species richness model.

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